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ANALYSIS OF GROWTH OF THE RED-TAILED HAWK[1]

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ABSTRACT. Analysis of anatomical measurements of 14 red-tailed hawks, *Buteo jamaicensis,* was characterized by positive allometry in the increase in body weight. Intraspecific variation up to 22% was observed in the cumulative increase in body weight. Females were statistically larger than males in body weight and length of seventh primary, but not in length of tarsus, third toe, and culmen. No yearly statistical differences were found in the growth rates. Weekly growth gains show the culmen, toes and tarsus develop during the first 2 weeks while growth gains in body weight and primaries are fastest during weeks 3 and 4, respectively. Body weight was a good indicator of age up to the 24th day and length of the seventh primary was the best indicator of age after 24 days.

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INTRODUCTION

Although growth in birds recently has received considerable attention (*e.g.*, Ricklefs 1973, 1982; Werschkul and Jackson 1979), little quantitative data exist on the growth and development of falconiformes in general, and red-tailed hawks (*Buteo jamaicensis*) in particular. Sumner (1929) recorded changes in body weight in 4 nestlings but reported no information on other growth parameters. Imler (1937) and Fitch *et al.* (1946) reported qualitative information on body weights. Olendorff (1971) examined 15 different growth parameters and found 5 best for aging nestling hawks. In view of Olendorff's work on captive birds and the lack of quantitative growth information on wild falconiformes, this study was undertaken to analyze growth data from 4 nesting seasons for red-tailed hawks in central Ohio. We attempted to elucidate the following: examine weight and other characters such as bill size as a measure of growth; relate maximum growth periods to nestling behavior; and use those external measurements as an indication of age of the nestlings.

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METHODS AND MATERIALS

During the springs of 1975, 1976, 1977 and 1980 we measured growth parameters of 14 nestling red-tailed hawks 2/4, 1/2, 2/3, 2/5 (broods/individuals). Nests were selected during raptor censuses conducted in Butler, Delaware and Greene counties, Ohio.

A modified mirror and pole device was used to obtain information on clutch size. The hatching day of the chicks was discovered by direct observation of pipping. First and second nestlings were color-marked for individual recognition and measured daily from day 1 through fledging (about 42 days posthatching; Springer and Kirkley 1978). We determined sexes from differences in body weight and length of seventh primary just prior to fledging.

Five growth parameters were selected for study. Body weights were measured with Pesola spring scales. Lengths of the culmen, tarsus and third toe, and seventh primary were taken daily with dial calipers to the nearest 0.01 mm.

The components of nestling growth patterns (*i.e.*, form, rate, and magnitude) were first described quantitatively by the constants of equations which were fitted to the logistic growth curve (Ricklefs 1967, Olendorff 1971).

$$Wt = \frac{a}{1 + be^{-Kt}}$$

where Wt is the weight at age t, e is the base of the natural logarithm, a is the juvenile asymptote or final weight achieved, and K and b are fitted constants. K is proportional to the growth rate and b is inversely related to weight at time $t = 0$. The equation and the asymptote were selected to give the straightest converted line, and the constant K was calculated for the slope of this line. The growth constant (K) can be compared among species whose growth curves are fitted by the same equation.

An inverse measure of growth (T_{10-90}; Ricklefs 1967) permits a comparison of growth rate among species whose growth curves are fitted by different equations. The T_{10-90} growth index represents the time (days) required for growth between 10 and 90% of the asymptote. For linear measurements which exceeded 10% but not 40% of the asymptote at hatching, a growth index T_{40-90} (Olendorff 1971) was used. These values are obtained directly from the data. The highest value for each parameter attained by the nestlings was used as the asymptote. This gives adequate linearity for the curve-fitting process and eliminates subjective decisions with regard to the choice of asymptotic values (Olendorff 1971).

We analyzed data for sexual dimorphism using student-t-tests and analysis of variance. The resulting statistics were considered significant at $P < 0.05$.

RESULTS

All linear anatomical measurements plotted against body weight produced straight lines on a log-log plot. All body parts measured during this study increased in magnitude relatively faster than body weight. As the size of the whole organism increased, there was a progressive change in the absolute proportions of the body parts.

DAILY GROWTH. The general pattern of daily growth of nestling red-tailed hawks was sigmoid for all 5 parameters and consisted of a lag phase, logarithmic phase, decay phase, and asymptotic phase. In most linear parameters, the lag phase was not very pronounced or was absent.

Body weight was 57.6 ± 0.9 g at hatching. Females reached a 16% higher body weight asymptote than the males, and the growth indicators (T_{10-90}) and growth constant (K) showed females grew significantly for a longer period of time than males (table 1). Sexual dimorphism was not apparent until about 29 days of age (T, $P < 0.05$).

Growth of the culmen was rapid, essentially linear with age from day 1 to day 25, and leveled off at about 23 mm (table 1). At hatching, culmen length varied from 6.5 to 7.8 mm. No sexual dimorphism was found, and the asymptotes and growth constants of both sexes were similar statistically.

At hatching, the tarsus varied from 17 to 22 mm, grew rapidly and reached full nestling length by day 28. Although the tarsus of females was slightly larger than males ($F = 2.17$; $P < 0.14$), growth constants and indicators were similar between sexes (table 1).

Growth of the third toe was rapid. At hatching the third toe averaged 11 mm for both sexes and the time for toes to reach maximum lengths was not significantly different between sexes.

The seventh primary emerged on day 9. Growth was rapid and essentially linear with age from day 12 to fledging. Sexual dimorphism was evident from the third week until fledging. Primaries of females were significantly larger ($F = 5.96$; $P < 0.01$) than those of males (table 1). Primaries of males had significantly larger growth constants than females, but had similar growth indicators. Females reached an 8% higher asymptotic value than males. Less than 7% variation in feather length was found among individuals of each sex.

TABLE 1

Summary of average weights, linear dimensions and growth characteristics of 8 male and 6 female nestling red-tailed hawks.

Growth Parameters	Males	Females
Body Weight (g)		
Hatching	57	58
% Juvenile Asymptote (a)	5.9	5.0
Asymptote (a)	962	1149 *
Growth Constant (K) × 10^3	175	142 *
Growth Indicator (T_{10-90}) (days)	25	34 *
Culmen (mm)		
Hatching	6.5	7.3
% Juvenile Asymptote (a)	28.6	35.9
Asymptote (a)	22.7	23.0
Growth Constant (K) × 10^3	123	130
Growth Indicator (T_{40-90}) (days)	24	23
Tarsus (mm)		
Hatching	20.4	20.3
% Juvenile Asymptote (a)	24.0	23.4
Asymptote (a)	84.9	86.6
Growth Constant (K) × 10^3	132	123
Growth Indicator (T_{40-90}) (days)	18	22
Toe 3 (mm)		
Hatching	11.0	11.0
% Juvenile Asymptote (a)	23.7	23.2
Asymptote (a)	46.4	47.3
Growth Constant (K) × 10^3	167	139
Growth Indicator (T_{40-90}) (days)	17	19
Primary 7 (mm)		
Hatching	—	—
% Juvenile Asymptote (a)	—	—
Asymptote (a)	197	210 *
Growth Constant (K) × 10^3	239	208 *
Growth Indicator (T_{10-90}) (days)	32	32 *

*Significant difference (F, $P < 0.05$) between sexes

GROWTH AS A PERCENT OF ASYMPTOTE. To examine aspects of allometric growth not explicit in the daily growth indicies, we analyzed weekly measurements for both sexes as cumulative percentage of the juvenile asymptote (table 2). We averaged measurements of the culmen, third toe and tarsus for both sexes. Sexual dimorphism was only significant in body weight and seventh primary. These values represent weekly age standards by which age predictions (±2 days) can be made in the field. At hatching body weight averaged about 5.4% of the juvenile asymptote. The tarsus, third toe and culmen grew at similar rates each week, and were 24, 23, and 30% of their respective asymptote at hatching. They achieved about 90% of their nestling size by the fourth week. Seventh primaries reached 8% of their asymptote by the end of the second week and increased in steady weekly increments of approximately 20–30% of the asymptote until fledging.

GROWTH AS ACTUAL GAIN OR LOSS. Weekly asymptotic ratios are directly correlated with actual gains in weight and length, but actual gains illustrate maximum growth periods better (fig. 1). While weight gain in the first, second, and third weeks showed sharp steady increases (142 g, 234 g, and 270 g), weight gain in the fourth week slowed to 181 g. This decrease in weight gain correlated in time with the beginning of the decay phase (day 25). During the fifth and sixth weeks the actual gains were 66 g and 28 g, respectively. This decrease continues as individuals reach their juvenile asymptotic plateau.

The culmen increased 4.5, 4.1, and 3.7 mm the first, second and third weeks and growth slowed to less than 1 mm each week thereafter. The tarsus increased 14.5, 14.3, 14.5, and 13.6 mm during the first four weeks and growth slowed considerably during the fifth and sixth weeks.

The third toe increased 7.96, 10.9, and 8.4 mm in the first, second and third

TABLE 2

Cumulative increase in weight and linear measurements of nestling red-tailed hawks, represented as age standards and as a percentage of asymptote achieved prior to fledging. Asymptote calculated as the combined adult male and female mean measurements.

Growth Parameters	Time (Weeks) 0 M	0 F	1 M	1 F	2 M	2 F	3 M	3 F	4 M	4 F	5 M	5 F	6 M	6 F
Body Weight (g)	57	58	190	209	431	436	693	714	868	875	934	980	962	1146.7
Average	57.6	±0.9	191.3	±21.5	433.7	±30.8	681.7	±11.9	868	±35.1	960.0	±29.7	1050	±97.3
% of Asymptote	5.4		18.1		41.0		64.5		86.1		92.0		97.0	
Tarsus (mm)	20.4	20.3	35.2	35.5	51.4	48.8	64.1	65.7	78.4	78.9	83.2	83.9	84.0	86.6
Average	20.5	±1.7	35.1	±3.4	50.4	±3.9	64.1	±3.3	78.4	±1.9	83.6	±0.7	85.3	±1.2
% of Asymptote	23.9		41.0		58.8		74.7		91.4		97.0		99.0	
Toe 3 (mm)	11.0	11.0	16.9	16.4	30.4	25.8	37.2	36.6	41.7	41.6	43.9	44.2	46.4	47.3
Average	10.8	±0.7	16.9	±2.0	27.9	±3.1	37.0	±1.7	41.7	±0.5	43.6	±0.7	46.7	±0.7
% of Asymptote	23.0		36.0		59.5		78.9		88.9		92.9		99.6	
Culmen (mm)	6.5	7.3	12.2	12.4	15.3	15.9	19.1	19.7	21.1	21.5	22.4	22.5	22.7	23.0
Average	7.0	±0.5	11.5	±0.6	15.6	±0.8	19.3	±0.7	21.5	±0.4	22.7	±0.5	22.8	±1.1
% of Asymptote	30.0		49.8		67.5		83.5		93.0		98.3		98.7	
Primary 7 (mm)	—	—	—	—	14.9	16.7	55.7	53.3	119.5	123.8	164.0	171.0	197.5	210.0
Average	—	—	—	—	15.7	±3.0	55.3	±6.1	116.9	±7.7	168.7	±4.0	203.5	±7.1
% of Asymptote	—		—		7.7		27.3		57.8		83.1		99.0	

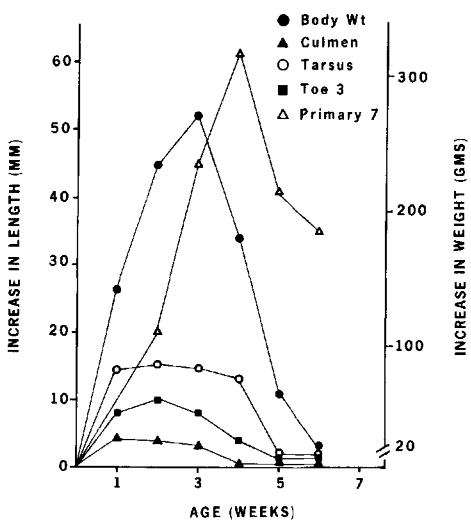

FIGURE 1. Weekly gains in weight and linear measurements of the nestling red-tailed hawks. Points represent average values for males and females.

weeks, after which growth gradually decreased. The seventh primary exhibited increased growth of 20.9, 45.4, and 61.5 mm during the second, third and fourth weeks and decreased gradually (41 and 35 mm) until fledging.

DISCUSSION

In comparing body weights reported by Olendorff (1971) and Fitch et al. (1946), and our study (table 3), less than 5% difference was found in growth constants (*K*) and asymptotes. Females in our study took 22% (8 days) longer to reach full nestling size than did females from Fitch et al. (1946) and 9% (3 days) longer than Olendorff's single captive female. Our average growth constants for the tarsus and third toe were significantly lower than Olendorff's values. We found the tarsus and third toe of males grew several

TABLE 3

Comparisons of asymptotes (a), growth constant (K) and growth indicators $T_{10\text{-}90}$ and $T_{40\text{-}90}$.

Growth of Parameters	Males: This Study	Males: Olendorff 1971	Males: Fitch et al. 1946	Females: This Study	Females: Olendorff 1971	Females: Fitch et al. 1946
Body Weight (g)						
Asymptote (a)	963	950	920	1147	1206	1175
Growth Constant (K) $\times 10^3$	176	173	200	162	171	168
Growth Indicator ($T_{10\text{-}90}$)	25	25	22	34	31	26
Tarsus (mm)						
Asymptote (a)	84.9	86.9	—	86.6	86.6	—
Growth Constant (K) $\times 10^3$	132 *	160	—	123	163	—
Growth Indicator ($T_{40\text{-}90}$)	18	16	—	22	16	—
Toe 3 (mm)						
Asymptote (a)	46.4	49.6	—	47.3	58.3	—
Growth Constant (K) $\times 10^3$	161 *	205	—	138 *	223	—
Growth Indicator ($T_{40\text{-}90}$)	17	13	—	19	12	—

*Significant difference (F, $P < 0.05$)

days faster than females which is also different from Olendorff's findings.

Our average growth constants were also significantly ($P < 0.05$) lower for culmen length than Olendorff's values. Differences in culmen values may be accounted for by differences in measuring technique. Our measurements were taken as an arch from where the culmen emerged from the cere to the tip of the upper mandible. Other possibilities could be sample size or health of the bird. Schreiber (1976) found starvation affected growth and development of the bill and tarsus in brown pelicans (*Pelecanus occidentalis*)

Growth proceeds towards genetically and environmentally determined plateaus or asymptotes. The asymptote is the final value (e.g. weight) obtained by the growing organism. This parameter is more accurately designated as the juvenile asymptote, and may be related to adult weight in 3 different ways. The most typical growth curve is one in which growth levels off at approximately adult values during the nesting period (cedar waxwing, *Bombycilla cedrorom,* Putnam 1949). In the second type of growth curve, the young attain peak values higher than the adult (barn swallow, *Hirundo rustica,* Ricklefs 1967). In the third type of growth curve, the young attain peak values that are below the adult (golden eagle, *Aquila chrysaetos,* Sumner 1929). Ricklefs (1967) found male red-tails followed the second pattern of growth, while females followed the third pattern. His male juvenile asymptote was slightly higher than adult values (J/A ratio of 1.04; Ricklefs 1967). In contrast, his female J/A ratio was 0.92.

When calculating J/A ratios and comparing them with other studies (table 4), both juvenile males and females peak below their adult asymptotic levels. This was also true in our study where J/A ratios for males and females were 0.94 and 0.93 respectively. Although female J/A ratios were slightly higher than males in the other studies, our values were similar between sexes. With respect to weight, red-tails follow a growth curve where young attain peak values below those of adults.

The same appears true for growth of the culmen. Craighead and Craighead (1956) reported male and female adult asymptotes of 25.1 mm and 27.7 mm, respectively

TABLE 4

A comparison between juvenile asymptotes and adult values. a = *asymptote,* (n) = *the number of individuals used in the calculation.* J/A = *the juvenile to adult asymptote ratio.*

	Body Weights					
	Males			Females		
References	*a*	(*n*)	J/A	*a*	(*n*)	J/A
This study	963	(8)	0.94	1149	(6)	0.93
Fitch et al. 1946	920	(4)	0.90	1175	(4)	0.95
Olendorff 1971	950	(4)	0.93	1206	(1)	0.98

(N = 40). When using these asymptotes as adult standards, the J/A ratios for males and females in this study were 0.90 and 0.82, respectively.

No statistical differences were found between years in the growth rates. Although differences occur in the daily magnitude of the various growth parameters, no trends were observed. This is not to say that growth rates were inflexible to environmental factors. For example, during 1977, cold, blizzard conditions delayed the breeding chronology approximately 3–4 weeks as compared to that reported by Springer and Kirkley (1978). Growth rates in 1977 were generally slower in the early logarithmic phase but changed later, when weather conditions improved. The third toe best exemplifies this trend. Intraspecific variation up to 22% was observed in the cumulative increase in body weight.

Different periods of maximum gain in growth can be related to changes in energy allocation and correlated with behavioral changes of the nestlings. Maximum growth of the culmen in the first week reflects the developmental priority of the food consuming apparatus over other anatomical structures. Maximum growth of the toes during the second week corresponds to the maximum growth period of the tarsus and is associated with the general increase in activities and movement of the nestlings.

Maximum growth of the seventh primary occurs most rapidly during the last two weeks prior to fledging, while weight gains decline in the fourth week. During the fourth week, nestlings begin to stand upright on their feet rather than on their feet and knees, and begin feeding independently of parental guidance. Independent feeding behavior necessitates early development of the culmen, third toe and tarsus, for these trophic structures are essential to the mechanical manipulation of the food. This early development is further exemplified by the positive allometric relationship these structures have with respect to body weight. As the seventh primary undergoes continued rapid growth, the nestlings' energy allocation is channeled into feather development rather than into increasing weight. As the seventh primary develops, nestlings begin wing-flapping over the nest.

Body weight is useful in determining age in the early stages of growth, but once decay phase (approximately 24th day) is reached, reliability of weight measurements predicting age decreases substantially. Primary feathers of nestlings older than 23 days offer a complementary parameter for aging. Schreiber (1976) found wing length a good predictor of age in nestling brown pelicans. Schreiber suggests once the feathers begin to grow, the amount of resource allocation necessary for continued feather growth is considerably lower than that necessary to form the bone and other material involved in culmen growth. Hence, feather development is a good index for obtaining specific age of individual red-tails. Similarly, weight up to the decay phase is useful in determining relative age, whereas, past this point it better serves as an indicator of health in individual birds.

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